period. After the vacuoles reach the *trans* side of the stack, they migrate to the cell membrane, where the membrane of the vacuole merges with the cell membrane. There is then an opening of the joined membranes so that the contents of the vacuoles are released into the extracellular matrix without breaching the diffusion barrier provided by the cell membrane. Palade (1958b) originally termed this process "membrane fusion," but it was relabeled "exocytosis" by de Duve (1959).

Beyond tracing the course of protein transport, Jamieson and Palade set out to determine how tightly the processes of protein synthesis and transport are coupled and to identify the energy source for the process. Using cyclohexamide to block protein synthesis, Jamieson and Palade (1968a) were able to uncouple the synthesis of protein from its transport to the Golgi complex, showing that transport did not depend on new proteins entering the process. In a subsequent paper (Jamieson & Palade, 1968b), they addressed the energy requirements for the process by demonstrating that the glycolytic inhibitors (fluoride, iodoacetate) failed to block transport, but that respiratory inhibitors (N2, cyanide, antimycin A) and inhibitors of oxidative phosphorylation (dinitrophenol, oligomycin) did. Jamieson and Palade then speculated about what operation required energy:

> At present, it is clear that the energy is used to connect the RER cisternal space with that of the condensing vacuoles, and that the small peripheral vesicles of the Golgi complex participate in the connection. The details of this operation, however, remain obscure: the cell may establish intermittent connections between these two compartments or effect transport between them using the small peripheral vesicles as shuttle carriers. Both alternatives imply repeated membrane fission-fusion and this is most probably the energy-requiring event. (p. 599)

Jamieson and Palade clearly favored the hypothesis that small peripheral vesicles serve as shuttle carriers and that the nascent proteins remain membrane bound as they transverse the Golgi structure. Prior to their research, P. P. Grassé (1957), relying on early electron micrographs, had proposed a maturational or cisternal progression model according to which cisternae were continually being created on the *cis* side of the stack and matured as they moved to the *trans* side, where they disintegrated and released the newly synthesized products for further transport. Neutra and Leblond continued to espouse this view (Neutra & Leblond, 1969, p. 105), but in subsequent years evidence built for Palade's proposal and it became the dominate view.

Palade's early research did not focus on the Golgi stack, and to the degree that he investigated the function of the Golgi components, he focused on